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Morphology and taxonomy of the male *Kermes quercus* (L.) (*Homoptera, Coccoidea*)

[Pp. 193—216 and 4 text-figs.]

Morfologia i stanowisko systematyczne samca *Kermes quercus* (L.) (*Homoptera, Coccoidea*)

Морфология и таксономия самца *Kermes quercus* (L.) (*Homoptera, Coccoidea*)

Abstract. The morphology of the male *Kermes quercus* (L.) is described in detail and illustrated. On account of the constricted neck region and the association of the tentorial arms with the cranial apophysis, *Kermes* BOITARD belongs to the lecanoid *Coccoidea*. The morphology of the male confirms the status of *Kermesidae* as a dinstinct family. Among the lecanoid *Coccoidea* *Kermesidae* hold an intermediate position between the primitive families *Pseudococcidae* and *Eriococcidae* and the specialized *Coccidae* — *Lecaniodiaspididae* — *Asterolecaniidae*, but this does not mean that *Kermes* may be regarded as an annecting genus between the two groups. The resemblance between *Kermesidae* and the specialized groups of the lecanoid *Coccoidea* is due rather to convergence.

INTRODUCTION

The taxonomy of *Coccoidea* is based on the structure of the females. The males, which are much less available for study and in some species do not occur at all, have only occasionally been described, these descriptions including only certain fragments of the body structure.

THERON's study, published in 1958, concerning the body structure of the males of a few species representing different groups of *Coccoidea* indicated the possibility of utilizing the characteristics of the body structure of the males for the purpose of taxonomy. The most important contributions of his work are a description of the research method and the unification of the morphological terminology concerning the males.

Since this time several further studies have been published. Their authors, besides supplying detailed descriptions of the males of different families, have tried to solve the problem of the phylogeny of scale insects on the basis of the amassed comparative material. These include the studies of AFIFI (1968—17 species of *Pseudococcidae* and 7 of *Eriococcidae*), BEARDSLEY (1962 — some species of *Pseudococcidae*), GHAURI (1962 — 24 species of *Diaspididae*), GILIOMEE (1961 — 3 species of *Pseudococcidae*, 1967 — 23 species of *Coccidae*, 1967 a — *Lecaniodiaspis* TARG.-TOZZ., 1968 — *Asterolecanium* TARG.-TOZZ.), KOTEJA (1969 — *Psilococcus* BORCHS., 1970 — *Vittacoccus* BORCHS., both the species of the family *Coccidae*), KOTEJA, ROŚCISZEWSKA (1970 — *Parafairmairia* CKLL. of *Coccidae*), THERON (1962 — *Phenacoleachia* CKLL., 1968 — *Apiomorpha* RÜBSAAMEN and *Opisthoscelis* SCHRADER).

Here follows a morphological description of the male *Kermes quercus* L. and a discussion of the taxonomic status of the family *Kermesidae* within the lecanoid *Coccoidea*. Both the description of the body structure and the analysis of the characteristics are based on the schemes established in the studies of the above mentioned authors.

The male *Kermes quercus* (L.), like the males of other species of this genus, have not so far been studied in detail, although in a few studies some descriptions of their morphological structures can be found, mainly those of the head, antennae, and genital segment. JANCKE (1955) and BORCHSENIUS (1960) wrote about the males *Kermes quercus* (L.), KUWANA (1931) about *Kermes nakagawae* KUW., MCCONNEL and DAVIDSON (1959) about *Kermes pubescens* BOGUE.

From these studies it appears that in all studied species of the genus *Kermes* there are present five pairs of simple eyes, one pair of ocelli, 10-segmented antennae, a large membranous area of scutum, hamulohalterae with one seta, and an elongated penial sheath.

Material: 15 specimens of *Kermes quercus* (L.) collected on *Quercus robur* L. on May 18, 1970 at Łańcut, Poland.

MORPHOLOGY OF THE MALE *KERMES QUERCUS* (L.) [1]

General appearance

Living specimens reddish-brown, moderately robust, of medium size; when mounted 1600—2050 (1875) μm long, 430—500 (471) μm wide at mesothorax and 3070—3700 (3374)[2] μm wing expanse. Antennae and legs comparatively short. Dermal structures: antennae and legs with fleshy and hair-like setae; the two types of setae hard to differentiate; body itself with hair-like setae only; disc pores, excluding the pores in abdominal glandular pouches, absent.

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[1] As far as nomenclature is concerned, the authors have accepted the opinion of MORRISON and MORRISON (1966), giving full rights to the name *Kermes* in the zoological nomenclature and rejecting the late substitute names: *Kermococcus* SILVESTRI and *Talla* HEYDEN.

[2] The averages have been calculated from the values obtained for 10 specimens.

Head

Head in dorsal view subtriangular, rounded in lateral view. Anterodorsal bulge and ventral preocular depression absent. Length from apex to pronotal ridge 230—260 (344) μm, width across genae 270—300 (284) μm.

Dorsomedial part of epicranium (median crest, GILIOMEE, 1967) is membranous, not reticulated, posteriorly bounded by a distinct, postoccipital ridge. This ridge is present in most male *Coccoidea*, being absent only in the margaroid genus *Steingelia* (THERON, 1958) and the family *Coccidae* (GILIOMEE, 1967) except for *Parafairmairia gracilis* GREEN in which recently a distinct postoccipital ridge was found (KOTEJA, ROŚCISZEWSKA, 1970). Behind the postoccipital ridge occurs a bifurcate, strongly sclerotized plate which is considered to be a vestige of the postocciput.

Midcranial ridge Y-shaped, represented by short ventral and lateral arms at the apex of the head; dorsal arm absent or only marked by a band of weak sclerotization.

Preocular and postocular ridges well separated; the ventral arms of the former very long, meeting medially, the latter not forking below the ocellus. Ocular sclerites large, strongly sclerotized dorsally, but ventrally only around the eyes, not reticulated. Five pairs of simple eyes present: dorsal and ventral pairs subequal, about 40 μm in diameter, lateral ones smaller about 30 μm in diameter; ocelli present, small.

Genae dorsally weakly sclerotized, not reticulated.

Preoral ridge slender but distinct, latero-posteriorly connected to the postocular ridge by means of small triangular plates. The non-functional mouth opening small, situated behind or on apex of a comparatively large mouth tubercle. Such a tubercle has been described only in some males of *Eriococcidae* (AFIFI, 1968). Cranial apophysis short, not reaching the level of the ventral simple eyes, bifurcated. Tentorial bridge stout, posterior tentorial arms and pits present, anterior arms meeting the cranial apophysis separately.

Dorsal head setae 13—23 (18) occur on the dorsomedial part of epicranium; ventral setae 28—42 (33) on the area anterior to the preocular ridges, two of them being much longer than the rest; genal and ocular setae absent.

Antennae filiform, 10-segmented, 630—760 (700) μm long, i. e. about as long as 1/3 of the body length (the ratio being about 1:2.8) and slightly shorter than the hind legs (the ratio being about 1:1.1); lengths of segments in μm: I — 40—50, II — 45—60, III — 100—140, IV — 75—100, V — 75—90, VI — 72—100, VII — 72—80, VIII — 50—70, IX — 40—60, X — 48—50.

Scape about as wide as long, with 3—6 hair-like setae; pedicel as wide as long, with 9—19 setae and a sensillum placodeum; flagellar segments 30—40 μm wide; segment III being the longest, cylindrical, with 28—43 setae and 2—3 sensilla basiconica; segments IV—VI subequal, cylindrical, with 20—39 setae; segments VII—IX, the shortest, are barrel-shaped, with 14—40 setae (on segments VIII and IX one of them is an antennal bristle); terminal segment

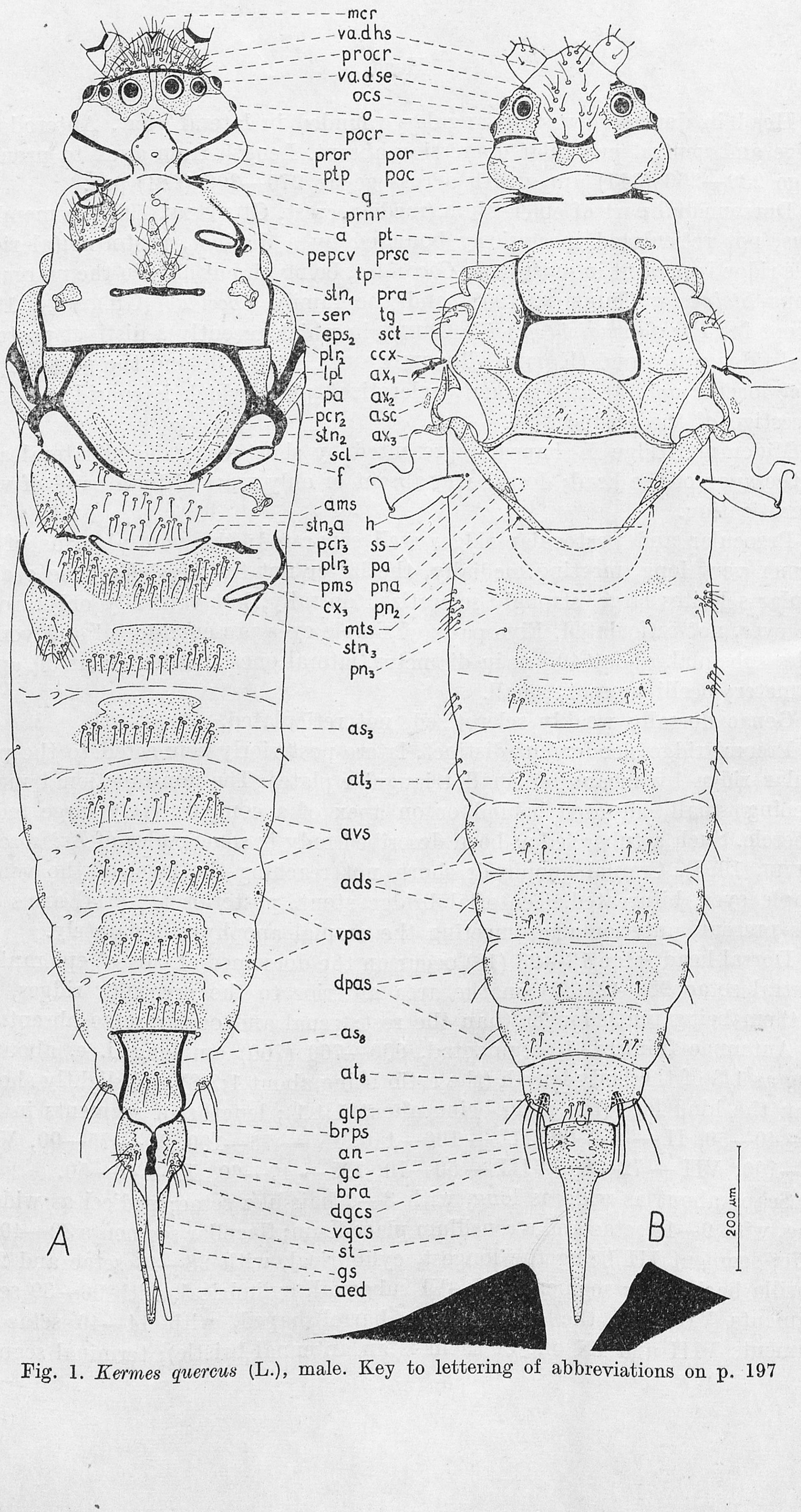


Fig. 1. *Kermes quercus* (L.), male. Key to lettering of abbreviations on p. 197

KEY TO LETTERING OF FIGURES 1—2

A.	ventral view
B.	dorsal view
C.	lateral view
D.	antenna
E.	posterior leg
F.	wing

a	structure of uknown homology
ads	abdominal dorsal setae
aed	aedeagus
ams	anterior metasternal setae
an	anus
as_{2-8}	abdominal sternites
asc	additional sclerite
at_{1-8}	abdominal tergites
avs	abdominal ventral setae
ax_{1-3}	axillary wing sclerites
bas	basalare
bra	basal rod of aedeagus
brps	basal ridge of penial sheath
ccx	costal complex of wing veins
cx	coxa
dgcs	dorsal setae of genital capsule
dhs	dorsal head setae
dpas	dorsopleural setae of abdomen
dse	dorsal simple eye
epm_3	metepimeron
eps_2	mesepisternum
eps_3	metepisternum
f	furca
g	gena
gc	genital capsule
glp	glandular pouch
gs	setae of style
h	hamulohaltere
lpl	lateropleurite
mcr	midcranial ridge
mr	marginal ridge
mt	mouth tubercle
mts	metatergal setae
o	ocellus
ocs	ocular sclerite
pa	postalare
pcr_2	precoxal ridge of mesothorax
pcr_3	precoxal ridge of metathorax
pepcv	proepisternum+cervical sclerite
plr_2	mesopleural ridge
plr_3	metapleural ridge
pms	posterior metasternal setae
pn_3	metapostnotum
pna	postnostal apophysis
poc	vestiges of postocciput
pocr	postocular ridge
por	postoccipital ridge
pra	prealare
prnr	pronotal ridge
procr	preocular ridge
pror	preoral ridge
pt	posttergite
ptp	posterior tentorial pit
pwp	pleural wing process
sa	subalare
scl	scutellum
sct	scutum
ser	subepisternal ridge
ss	suspensorial sclerite
st	style
stn_1	prosternum
stn_2	basisternum of mesothorax
stn_3	metasternum
stn_3a	metasternal apophysis
tg	tegula
tp	triangular plate
v a. dhs	ventral and dorsal head setae
v a. dse	ventral, lateral and dorsal simple eyes
vgcs	ventral setae of genital capsule
vhs	ventral head setae
vpas	ventropleural setae of abdomen
vse	ventral simple eye

barrel-shaped, with 3—5 capitate sensory setae, 3 antennal bristles, 4—15 fleshy setae and 2 sensilla basiconica. On the flagellar segments fleshy setae are more numerous than the hair-like ones but the two types of setae are not always distinct.

Thorax

The thorax is separated from the head by a deep cervical grove. Its length from pronotal ridge to mesopostphragma 480—650 (541) μm.

Prothorax. Pronotal ridge medially interrupted by weak sclerotization. Lateral pronotal sclerites indistinct, posttergites small. Proepisternum-cervical sclerite is dorsally approached by the pronotal ridge and anteriorly articulates with the postocular ridge; posteriorly it is connected with the pleural ridge, which carries a small pleural apophysis. Proepimeron indistinguishable. Prosternum triangular, sclerotized, not reticulated; prosternal transverse ridge distinct. In some specimens a small apophysis is situated medially in the membrane anterior to the prosternum. This structure was also found in *Phenacoleachiidae* (Theron, 1962), some *Coccidae* (Giliomee, 1967), and *Lecaniodiaspis* (Giliomee, 1967 a). On the prosternum 8—10 hair-like setae present; other regions of prothorax without setae.

Mesothorax. In *Kermes quercus* (L.) the mesothorax resembles that of the families *Coccidae* and *Lecaniodiaspididae*. The mesotergum is divided into alinotum (prescutum, scutum, and scutellum) and postnotum.

The prescutum has the shape of a large median bulge, laterally bounded by the prescutal ridges which extend posteriorly to the scutellum along the membranous area of scutum; the posterior margin is formed by the prescutal suture. It is strongly sclerotized, not reticulated, 90—100 (97) μm long and 190—210 (200) μm wide.

The scutum is represented by two strongly sclerotized lateral plates separated medially by the subrectangular membranous area. This membrane, 90—100 μm long and 180—200 μm wide, is also found in other *Coccoidea*, e. g. some *Margarodidae* (Theron, 1958), the *Coccidae* (Giliomee, 1967), the *Lecaniodiaspididae* (Giliomee, 1967 a), and the *Asterolecaniidae* (Giliomee, 1968). In the anterior region the scutum gives rise to the prealare which articulates by means of a heavily sclerotized triangular plate with the episternum; laterally it bears an anterior notal wing process and posteriorly a posterior notal wing lobe.

The scutellum is comparatively large (75—100 μm long, 170—200 μm wide), its anterior and posterior edges curve sharply inwards but they do not unite internally. A large membranous area separates it from the postnotum. The latter is partly overlapped by the metathoracic fold. Laterally it is prodduced into a broad postalare which articulates anteriorly with the pleural ridge and is dorsally connected to the posterior marginal fold of the alinotum and the axillary cord of the wing.

The mesopleural ridge is strong, following an oblique course across the pleuron. Ventrally it forms a process for articulation with the coxa and dorsally it joins the rounded, comparatively large pleural wing process. The basalare is well developed and connects the pleural wing process with the episternum; the subalare is small. The episternum consists of two sclerites completely sepa-

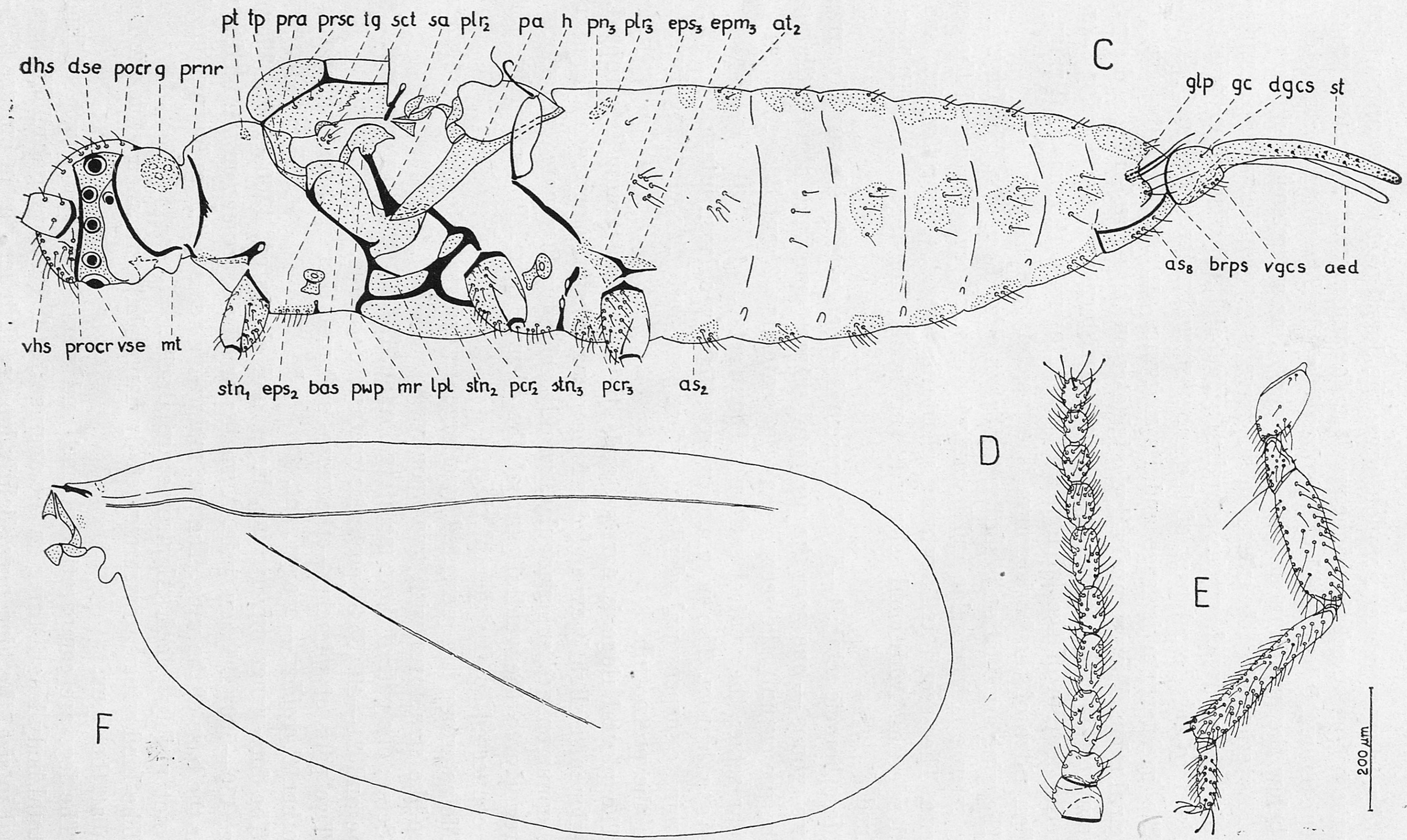


Fig. 2. *Kermes quercus* (L.), male. Key to lettering of abbreviations on p. 197

rated by a transverse membranous area; the dorsal part is large and articulates with the triangular sclerite of the prealare, the ventral part is vestigal; anteriorly the episternum is bounded by the subespisternal ridge, which is strong dorsally but below the membranous cleft only marked as an extension of the precoxal ridge. Anteriorly to this extension lies large lateropleurite, which is anteriorly bounded by a branch of the marginal ridge of the basisternum; this branch is joined to the dorsal part of the subepisternal ridge. Epimeron absent.

The basisternum is large and its margines are reinforced by the strong marginal ridge. The precoxal ridge originates on the pleural ridge and stretches posteroventrally along the margin of the basisternum to the furcal pit; on the posterior margin of the lateropleurite it unites with the marginal ridge. The median ridge of the basisternum is completely absent.

The wing articulation is similar to that in other *Coccoidea*. The first axillary wing sclerite is triangular and its anterior arm not curved around the second sclerite. The second axillary wing sclerite is narrow, joining the first and the third sclerites. Additional sclerite is very weak. The tegula is small but well defined.

Mesothoracic setae: 1—5 (3.3) prescutal setae on each side, usually arranged in two groups — one near the prescutal suture (sometimes also on the margin of the prescutum), the second near the scutellum; 2 scutellar setae; 2—5 (3.6) tegular setae; the ventral surface without setae.

Metathorax. The notum is represented by a large internal sclerite and two minute suspensorial sclerites. Further posteriorly two subtriangular sclerites form the postnotum.

The pleural ridge is narrow, and above the episternum interrupted. Its anterior end is slightly expanded to form a small pleural wing process. Episternum and epimeron are subtriangular, weakly sclerotized, situated anteriorly and posteriorly to the ventral part of the pleural ridge. Precoxal ridge strong, not connected to the pleural ridge.

Metasternum is represented by a large, transverse plate and some transverse ridge-like structures with two apophyses.

Setae: one pair of short metatergal setae; 12—28 (16.4) anterior metasternal setae and 28—40 (35.3) posterior metasternal setae.

Two pairs of spiracles — the meso- and metathoracic ones similar to those in other *Coccoidea* — are present.

The fore wings are hyaline, large, and elongated, 1300—1600 (1430) μm long, 450—590 (496) μm wide. A small alar lobe is present on the hind margin near the base of the wing. The two main wing veins — the radius and media — are not visibly joined. Alar setae are absent.

The hind wings are represented by hamulohalterae, each with one hooked seta at the apex.

The legs are comparatively short and stout; the ratio length of hind leg to total body length being on the average 1:2.4. The fore and middle legs subequal in size, the hind ones slightly longer; their lengths in μm are 650—790

(733), 690—780 (730) and 690—850 (780) respectively. Coxa 75—90 μm long, with 17—30 setae. Trochanter and femur well separated, the former 60—90 μm long, about 30 μm wide, with 15—22 setae (one apical seta and two small needle-like setae on the basal ridge distinct) and 3 pairs of oval campaniform sensilla. Femur 180—230 μm long, 40—60 μm wide, with 42—60 setae. Tibia 210—310 μm long, about 30 μm wide with 67—113 setae and 2 distinct apical spurs. Tarsus 2-segmented, the basal segment being very short; 80—100 μm long, about 20 μm wide, with 19—30 setae; tarsal digitules apically knobbed, 35—45 μm long; a single campaniform sensillum is situated dorsally near the base of the tarsus. Claw about 30 μm long, with a very small denticle on the plantar surface; ungual digitules apically knobbed, slightly longer than the claw.

Abdomen

The abdomen is composed of eight pregenital segments and the ninth genital one. The presence of large, sclerotized plates on each dorsal and ventral surfaces — the tergites and sternites—make the segmentation fairly distinct. It is 700—850 (768) μm long, 360—500 (447) μm wide.

The tergites and sternites of the II—VII abdominal segments are represented by large, subrectangular plates. The tergite on segment VIII does not differ from those of the anterior segments; the sternite is laterally reinforced by heavily sclerotized ridges which extend far posteriorly and seem to be articulated laterally with the penial sheath, while anteriorly they are connected with a transverse ridge. Among the lecanoid males similar but not so strong sclerotizations on the ventral surface of the VIIIth abdominal segment are described in *Eriococcus buxi* (Fonscolombe) and *E. orariensis* Hoy (Afifi, 1968). The pleural sclerotizations are present on the segments IV—VIII only. The caudal extension on segments VI—VII is lacking.

Taking into consideration the sclerotization of the abdomen of the male, *Kermes quercus* (L.) is one of the strongest sclerotized species which have so far been investigated, only some males of the *Margarodidae* and *Coccidae* being similarly well sclerotized.

The segments bear hair-like setae in the following numbers: 2—4 tergal setae on segments I—II, 4 on segments III—VII, and 4—5 on segment VIII; 11—21 sternal setae on segment II, 9—17 on segments III—IV, 5—12 on segments V—VII and 5—8 on segment VIII; pleural setae on segments III—VII are subdivided into dorsopleural and ventropleural ones, on segment I — 4—11 setae on each side, II — 2—6, III—VII — 3—4, on segment VIII — 3, of which one is much longer than the remaining ones.

Glandular pouch on segment VIII comparatively deep, with two long setae and some pores.

The general structure of the genital segment is similar to that of the *Coccidae*, *Lecaniodiaspididae*, *Asterolecaniidae*, and *Diaspididae* but also has some characters in common with the *Pseudococcidae* and *Eriococcidae*. It forms a heavily

sclerotized penial sheath which is distinctly divided into an anterior, cylindrical basal part (genital capsule) and a posterior, elongated conical one (style). Total length of the penial sheath 330—350 (338) μm, width at the base of the aedeagus 65—85 (64) μm; the ratio of its length to the total body length is on the average 1:5.5. Basal sclerotizations of the genital capsule are joined medially. The ventral slit-like opening is very long, and its edges are without any of the processes described in some *Pseudococcidae* (Afifi, 1968).

The anus opens on the dorsal surface on the base of the penial sheath and in the specimens trated with KOH it may be overlapped by a fold of the VIIIth abdominal tergite. The IXth and Xth tergites, described in some other male *Coccoidea*, have not been observed in *Kermes quercus* (L.); probably they are fused with the basal part of the penial sheath.

The aedeagus is 240—280 (256) μm long, not extending beyond the apex of the penial sheath. Basal rod heavily sclerotized, 50—80 (59) μm long; in ventral view it becomes narrowed anteriorly, and in the lateral view it is irregularly curved.

Setae and sensilla: the genital capsule bears one pair of dorsal setae and 4—7 ventro-pleural setae on each side; on the style there are 10—26 small setae which posteriorly become smaller, on the apex of the style occurs a cluster of small sensilla.

DISCUSSION

A. General remarks

Two principal conclusions can be drawn from the several years' discussion on the phylogeny of *Coccoidea* based on the structure of the males:

1. The studies on the males have not abolished Balachowsky's (1942, 1948) division of *Coccoidea* into three principal branches: margaroid, lecanoid, and diaspidoid groups, although certain strictures concerning this conception have been advanced. The same applies to the taxons on the family level established on the basis of the structure of the females. Not a single one of these taxons has been disputed, nor has any new taxon on this level, based on the male structure only, been established. The studies on the male have, however, introduced very great changes on the lower taxonomic levels, especially in affiliating genera into groups within the given families.

2. Each successive study, contributing new factual material to the discussion, revealed further and wider relationships between the families. Certain suggestions however, concerning the supposed phylogeny of *Coccoidea* do not seem convincing.

This results primarily from the fact that the studies on the males include a relatively small number of species. Each new description often introduces essential corrections of the previous views, and the number of characters formerly considered to be exclusive for the given groups is gradually reduced. Thus,

e. g., in the family *Coccidae*, which is relatively the best studied, out of 46 characters discussed in the present work, as many as 21 turned out to be alternative, which means that in as many as 21 cases characters considered to be characteristic for different families are present in some species of this family.

Besides, as far as the male scale insects are concerned it is difficult to define a given case whether a certain character is „primitive“ or „specialized“ owing to a much advanced reduction of many morphological structures. Thus, e. g., the postoccipital ridge, occurring in many groups, and the plate behind it may be interpreted either as a postoccipital ridge and postocciput of other insects, or, as Giliomee (1968) suggests new structures which have developed secondarily in *Coccoidea* and nonhomologically with the postoccipital region in other insects. Also developing of the membranous area of scutum may be considered to be a primitive character (Afifi, 1968) or specialized, as the authors of the present work suppose.

On the other hand many specialized characters have developed independently in different groups of *Coccoidea*, e. g. the reduction of hamulohalterae in *Rhizoecus* Künckel (*Pseudococcidae*), in many genera of the family *Coccidae* and *Asterolecaniidae.*

Finally, the tracing of the phylogeny of the scale insects on the basis of the structure of the males has not been done by finding out and investigating the evolution of the „important“ characters but by comparing the number of the shared and differentiating characters (numerical taxonomy).

Since, as it has already been mentioned, the material studied is very limited, the application of this method to scale insects is as little conclusive as that of pure speculation. It is to be hoped, however, that consistent collecting of the factual material will lead to positive results.

The authors are therefore persuated that their views as stated below concerning the family *Kermesidae* will be either corrected or rejected as a result of further studies.

B. The taxonomic status of the family *Kermesidae*

The male characters (only macropterous forms) shared by, and differentiating the families within the lecanoid group are presented in Tables I and II and in figures 3 and 4.

The data concerning the *Pseudococcidae* and *Eriococcidae* have been taken from the paper by Afifi (1968), the *Coccidae* from the papers by Giliomee (1967), Koteja (1969, 1970) and Koteja, Rościszewska (1970), and the *Lecaniodiaspididae* and *Asterolecaniidae* from the papers by Giliomee (1967 a and 1968 respectively).

The data concerning the males of the lecanoid group, published by other authors, are not complete and certainly could not be taken into consideration in the comparison of the families. Among others, the interesting genera *Puto* Sign. (Reyne, 1954 and Beardsley, 1962), *Macrocerococcus* Leonardi (Schmut-

Table 1

Statement of male characters separating families of the lecanoid *Coccoidea*

Characters	*Pseudococcidae* 1	*Eriococcidae* 2	*Kermesidae* 3	*Coccidae* 4	*Lecaniodiaspididae* 5	*Asterolecaniidae* 6
1. Male puparium: A — formed of fluffy waxy threads, B — formed of glassy waxy plates, C — of other structure	A	A	A	B	B	C
2. Body: A — robust, B — slender	B	A	A	AB	A	A
3. Fleshy setae on the body: A — absent, B — present	AB	A	A	AB	A	A
4. Disc pores on the body (excepting pores of the glandular pouch or plate): A — present, B — ent	AB	B	B	AB	B	B
5. Head in lateral view: A — rounded, B — flattened dorsoventrally, C — elongated dorsoventrally	AB	A	A	ABC	A	A
6. Dorsomedial part of epicranium: A — sclerotized, B — not sclerotized	A	A	B	AB	A	B
7. Postoccipital ridge: A — present, B — absent	A	A	A	AB	A	A
8. Vestiges of postocciput: A — present, B — absent	B	B	A	B	A	A
9. Midcranial ridge dorsally: A — present, B — absent	AB	A	B	B	B	B
10. Pre- and postocular ridges: A — separated, B — fused	AB	A	A	AB	A	A
11 Preocular ridge ventrally: A — very strong, continuous from side to side, B — weak, short, or absent	B	B	A	B	B	B
12. Ocular sclerite dorsally: A — well sclerotized throughout, B — sclerotized only around eyes	A	A	B	A	A	B
13. Number of simple eyes: A — more than 2 pairs, B — 2 pairs only	B	B	A	AB	B	B
14. Mouth tubercle: A — present, B — absent	B	AB	A	B	B	B
15. Cranial apophysis: A — truncate, B — furcated	A	AB	B	AB	A	A
16. Ocular setae: A — present, B — absent	AB	A	B	AB	B	B

Table 1. Continued

Characters	1	2	3	4	5	6
17. Genal setae: A — present, B — absent	A	A	B	AB	B	B
18. 3rd antennal segment: A — being the longest, B — shorter at least than some of the other segments	A	A	A	B	?	?
19. 9th antennal segment: A — barrel-shaped, B — cylindrical	B	A	A	B	B	B
20. 10th antennal segment: A — barrel-shaped, B — cylindrical C — apically constricted	C	C	A	BC	B	?
21. Membranous area of scutum: A — absent or very narrow, B — about as wide as prescutum	A	A	B	B	B	B
22. Mesepimeron: A — present, B absent	A	A	B	AB	A	B
23. Median ridge of basisternum: A — absent, B — present	A	A	A	AB	B	A
24. Metasternal apophysis: A — present, B — absent	A	A	A	B	B	B
25. Metasternal plate: A — large, B — vestigal or reduced	B	B	A	AB	A	A
26. Scutellar setae: A — present, B — absent	A	A	A	AB	B	B
27. Metasternal setae: A — present, B — absent	A	A	A	AB	A	B
28. Hamulohalterae: A — present, B — absent	A	A	A	AB	A	B
29. Tarsus: A — 2-segmented, B — 1-segmented	A	A	A	B	B	B
30. Apical spurs on tibia: A — 2 spurs present, B — 1 spur present, C — absent or not differentiated	A	A	A	B	B?	C
31. Tergites on abdominal segments II—VII: A — forming large plates on all segments, B — absent or very small and weak	B	B	A	AB	B	B
32. Sternites on abdominal segments II—VII: A — forming large plates on all segments, B — present only on some of them, or absent	B	B	A	AB	B	A
33. Pleurites on abdominal segments IV—VII: A — present, B — absent	B	B	A	AB	A	B
34. 8th abdominal sternite: A — represented by a large plate, B — represented by two small sclerites or absent	B	B	A	A	A	A
35. 8th abdominal sternite: A — reinforced by strong lateral ridges and anterior transverse one, B — only small lateral ridges present, or or ridges absent	B	B	A	B	B	B

Table 1. Continued

Characters	1	2	3	4	5	6
36. Ventral setae on abdomen: A — more numerous than the dorsal ones, B — subequal or less numerous than the dorsal ones	B	B	A	A	A	A
37. Glandular pouch or plate: A — present, B — absent	A	A	A	AB	B	B
38. Ratio width to length of penial sheath: A — penial sheath thick (ratio 1:3 or less), B — penial sheath slender (ratio 1:4 or more)	A	A	B	B	B	B
39. The style of penial sheath: A — subequal or shorter than the basal capsule, B — much longer than the basal capsule	A	A	B	B	B	B
40. Tergite 9+10: A — represented by a separate plate, B — fused with the genital capsule	A	B	B	B	B	B
41. Aedeagus: A — arising just behind the basal ridges of the genital capsule, B — arising at a great distance from the basal ring of the genital capsule	A	B	B	B	B	B
42. Aedeagus: A — subequal or longer than the style, B — distinctly shorter than the style	A	A	A	B	A	A
43. Aedeagus in lateral view: A — curved, B — straight	A	A	B	B	B	B
44. Anal opening: A — opened backwards, slit-like, B — rounded, well defined, opened upwards, C — indistinct, opened upwards	A	B	C	C	C	C
45. Dorsal setae on genital capsule on each side: A — more than 2 setae, B — 2 setae, C — 1 seta, D — no setae	A	B	C	D	D	C
46. Ventral setae on genital capsule on each side: A — more than 1 seta, B — 1 seta, C — no setae	A	A	A	C	C	B
Number of exclusive characters	4	2	3	1	0	3
Number of primitive characters	26	29	29	3	16	13
Number of specialized characters	14	15	17	22	29	31
Both conditions possible	6	2	0	21	0	0

TERER, 1952) *Rhizoecus* KÜNCKEL (SCHMUTTERER, 1952 and BEARDSLEY, 1962) and both *Apiomorpha* RÜBSAAMEN and *Opisthoscelis* SCHRADER (THERON, 1968) were omitted form the tables. The genera *Puto* and *Macrocerococcus* hold an extreme position among the *Pseudococcidae*, being the most primitive ones

(heavy sclerotization of the body, presence of numerous disc pores on the head, the ventral arm of the midcranial ridge very long, posteriorly reaching the preoral ridge, numerous simple eyes, etc.), whereas *Rhizoecus* is the most specialized genus (the head broadly joined to the thorax, absence of a distinct midcranial ridge, absence of lateral ocelli, hamulohalterae, glandular pouch, etc.). *Apiomorpha* and *Opisthoscelis*, two genera of uncertain taxonomic position, show some affinities with *Eriococcidae*.

The characters listed in Table I occur in two conditions — a primitive and a specialized one. Those, believed to be primitive are marked „A", and the specialized ones „B", „C", and „D", with regard to the direction and level of the specialization.

Table II contains the number of characters shared by and differentiating the pairs of families (columns 1—3). Column 4 represents the fraction of common characters in relation to the total number of compared ones. Characters which are partly common, i. e. occurring only in some members of the respective family and partly differentiating (the combinations A—AB, AB—B, AB—AB, and so on) were given a score of 0,5 unit each; e. g. *Eriococcidae* and *Kermesidae* share 21 characters and are separated by 23 characters, but 2 characters (Nos 14 and 15) occurring in *Kermesidae* are present also in some members of *Eriococcidae*; the number thus corrected will be 22 ($21+2\times0.5$) shared and 24 ($23+2\times0,5$) differentiating. The number of shared characters (22) was divided by the total number of the compared characters (46) and the result (0,49) was accepted as a measure of the similarity between the two families. These values were the basis for drawing the lines between the families in fig. 3.

In the same way, the ratio primitive characters to the total number of shared characters was calculated. When the given character occurs only in some members of the compared family, it was counted as 0.5, e. g. *Eriococcidae* and *Kermesidae* share 18 primitive characters and 1 occurring only in *Kermes* and in some genera of *Eriococcidae*, so the number of primitive characters shared by the two families is 18.5, and the shared specialized characters 2.5. The fraction of the shared primitive characters is, therefore, 18.5: (18.5+2.5) — 0.88 (Table II column 5). On the basis of these numbers figure 4 was drawn.

From the comparison of the characters shared by, and differentiating the families a number of conclusions concerning the systematic position of the family *Kermesidae* and the relationships within the lecanoid group can be drawn.

1. The genus *Kermes* Boitard was included by the majority of scholars with the genus *Eriococcus* Targ.-Tozz. and those related to it into one family or subfamily whose name was derived either from the genera *Kermes* or *Eriococcus* (Green 1922, Kiričenko 1930, Goux 1946, Ferris 1957, Hoy 1963). Some scholars include in this group also the genus *Dactylopius* Costa (the family *Dactylopiidae*, Fernald 1903); Balachowsky (1942) affiliates it with *Pseudococcidae*; still others look upon the genus *Kermes* as a separate, monotypical group on a family level (Maskell 1883, MacGillivray 1921, Borchsenius 1960).

Table II

Numbers of male characters shared by and separating the families of the lecanoid *Coccoidea*

Pairs of families	numbers of characters			fraction of	
	shared	exclusive	separating	shared characters	shared primitive characters
	1	2	3	4	5
1. *Pseudococcidae* — *Eriococcidae*	32	3	6	0.78	0.66
2. *Pseudococcidae* — *Kermesidae*	13	0	27	0.35	0.90
3. *Pseudococcidae* — *Coccidae*	10	0	17	0.40	0.42
4. *Pseudococcidae* — *Lecaniodiaspididae*	16	0	23	0.42	0.53
5. *Pseudococcidae* — *Asterolecaniidae*	11	0	26	0.33	0.39
6. *Eriococcidae* — *Kermesidae*	21	1	23	0.48	0.84
7. *Eriococcidae* — *Coccidae*	7	0	17	0.39	0.50
8. *Eriococcidae* — *Lecaniodiaspididae*	19	0	24	0.44	0.57
9. *Eriococcidae* — *Asterolecaniidae*	14	0	28	0.34	0.47
10. *Kermesidae* — *Coccidae*	10	0	15	0.44	0.46
11. *Kermesidae* — *Lecaniodiaspididae*	24	0	21	0.53	0.54
12. *Kermesidae* — *Asterolecaniidae*	26	1	18	0.59	0.46
13. *Coccidae* — *Lecaniodiaspididae*	21	3	2	0.71	0.28
14. *Coccidae* — *Asterolecaniidae*	16	0	7	0.61	0.24
15. *Lecaniodiaspididae* — *Asterolecaniidae*	31	0	12	0.73	0.35

The present study has shown that a) the genus *Kermes* without doubt belongs to the lecanoid *Coccoidea* (the neck region is constricted, the tentorium associated with the cranial apophysis), and b) the formation of a separate group for this genus is wholly justified by the structure of the males.

The genus under discussion is characterised by the following features, never before observed in the lecanoid group.

a. The preocular ridge is very strong ventrally and continuous from side to side, and the midcranial ridge is reduced to a short ventral arm and two lateral branches, forming a small Y-shaped figure between the antennae.

b. The loth antennal segment is barrel-shaped.

c. The 8th abdominal sternite is reinforced by very strong, longitudinal ridges which articulate posteriorly with the genital capsule, and an anterior transverse one.

Another important feature of the genus *Kermes* Boitard is heavy sclerotization of the abdomen — all the tergites and sternites are represented by large subrectangular plates, and pleural sclerotizations are present on segments IV—VII. Similar conditions have been found only in *Psilococcus* Borchs. (Koteja 1969) and, as far as lateral sclerotization is concerned, also in *Inglisia theobromae* Newstead (Giliomee 1967). But it may be noticed here that the heavy sclerotization of the abdomen is regarded in the *Coccoidea* as a primitive feature while *Psilococcus* Borchs. is a specialized genus in respect of both female

and male morphology; it is therefore possible that the sclerotization of the abdomen in *Psilococcus* Borchs. is of secondary nature.

2. Disregarding the value of the features and taking into account only the general number of common and differentiating characters, the following families can be considered as being closely related: *Pseudococcidae* to *Eriococcidae* (fraction of shared characters 0.78), *Lecaniodiaspididae* to *Asterolecaniidae* (0.73), and *Coccidae* to *Lecaniodiaspididae* (0.71) (Fig. 3).

3. In the same way all the families can be divided into two groups: *Pseudococcidae* — *Eriococcidae* (0.78) and *Coccidae* — *Lecaniodiaspididae* — *Asterolecaniidae* — *Kermesidae* (0.55—0.75 in particular pairs of families) (fig. 3).

4. The similarity of the pairs of families: *Lecaniodiaspididae* — *Asterolecaniidae*, *Coccidae* — *Asterolecaniidae*, *Coccidae* — *Lecaniodiaspididae*, and *Pseudococcidae* — *Asterolecaniidae* is based principally on the specialized characters (fig. 4), whereas that of the pairs *Pseudococcidae* — *Eriococcidae*, *Pseudococcidae* — *Kermesidae* and *Eriococcidae* — *Kermesidae* is based on the primitive characters.

However, it must be remembered here that because of the higher specialization of the families *Coccidae*, *Lecaniodiaspididae*, and *Asterolecaniidae* the fraction of shared specialized characters is also greater.

5. Taking into consideration both primitive and specialized characters, the genus *Kermes* holds an intermediate position between the groups *Pseudococcidae* — *Eriococcidae* and *Coccidae* — *Lecaniodiaspididae* — *Asterolecaniidae*.

With the former it shares the following primitive characters:

a. male puparium formed of fluffy waxy threads

b. metasternal apophysis present

c. tarsus 2-segmented

d. two apical spurs on tibia

e. numerous ventral setae on the genital capsule.

With the second group *Kermes* shares rather specialized characters:

a. the large membranous area of the scutum

b. the 8th abdominal sternite represented by a large transverse plate

c. ventral abdominal setae more numerous than the dorsal ones

d. penial sheath elongated and comparatively slender, with the style longer than the basal capsule

e. aedeagus in lateral view not curved

Giliomee's (1967) suggestion, according to which of all the lecanoid group *Kermesidae* were most closely related to *Coccidae*, has not been corroborated by the present study.

It is impossible in this study either to accept or reject Kosztarab's (1968) view that the family *Cryptococcidae* is an intermediate group between the families *Eriococcidae* and *Kermesidae*, since it was based on the female structure only, no studies of the males of the genera classed in this family having been done.

Recapitulating the results of the above discussion and taking into consideration the results of the previous studies on the females, the authors believe the

evolution of the discussed families of the lecanoid group to have occurred according to the following scheme.

The families belonging to this group are monophyletic. They evolved from the margaroid *Coccoidea*. The forms that were links between these two groups are so far unknown; probably they were closely related to the genera *Puto*

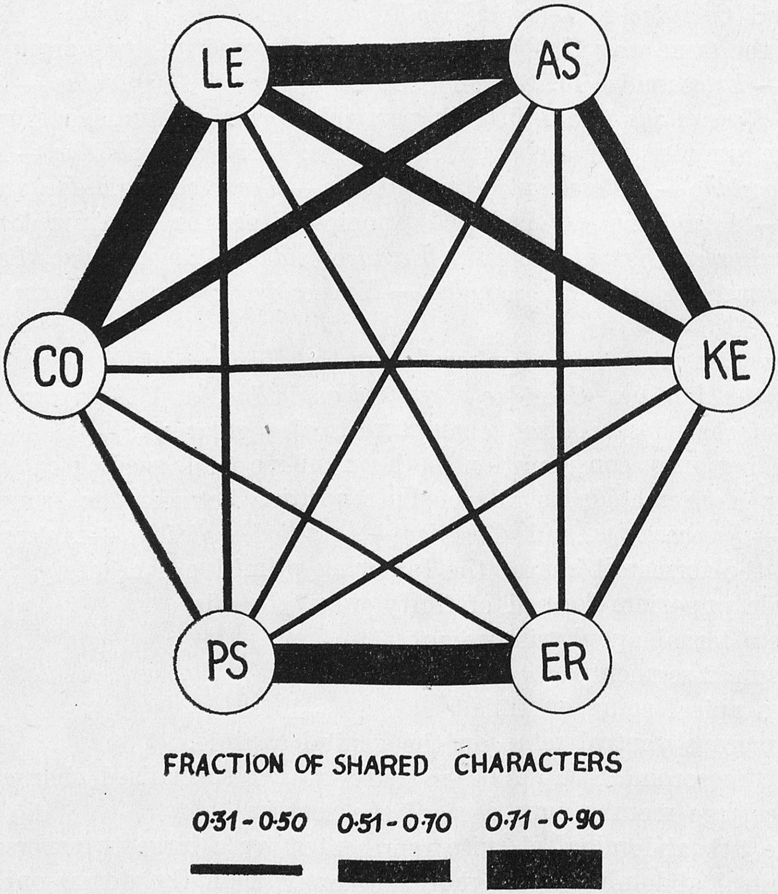


Fig. 3. The relationships between the families of the lecanoid *Coccoidea*. The width of the lines connecting the families resemble the fractions of the shared characters (see p. 9). AS — *Asterolecaniidae*, CO — *Coccidae*, ER — *Eriococcidae*, KE — *Kermesidae*, LE — *Lecaniodiaspididae*, PS — *Pseudococcidae*

and *Macrocerococcus*. The views of THERON (1962), GILIOMEE (1967), and AFIFI (1968), assuming that the *Coccidae* evolved from the margaroid *Coccoidea* through a form related to the *Steingelia* NASSONOV, and the *Pseudococcidae* independently through a form related to *Phenacoleachia* COCKERELL, and that therefore the lecanoid *Coccoidea* should be considered to be a polyphyletic group, seem to the authors unfounded. Although the male *Phenaco-*

leachia share numerous characters with the *Pseudococcidae*, and the male *Steingelia* with the *Coccidae*, these are, however, mostly specialized characters, whereas the true affinity should be sought for rather in the primitive ones. It would therefore seem more justified to recognize in the genera *Phenacoleachia* and *Steingelia* highly specialized members of the margaroid *Coccoidea* and their

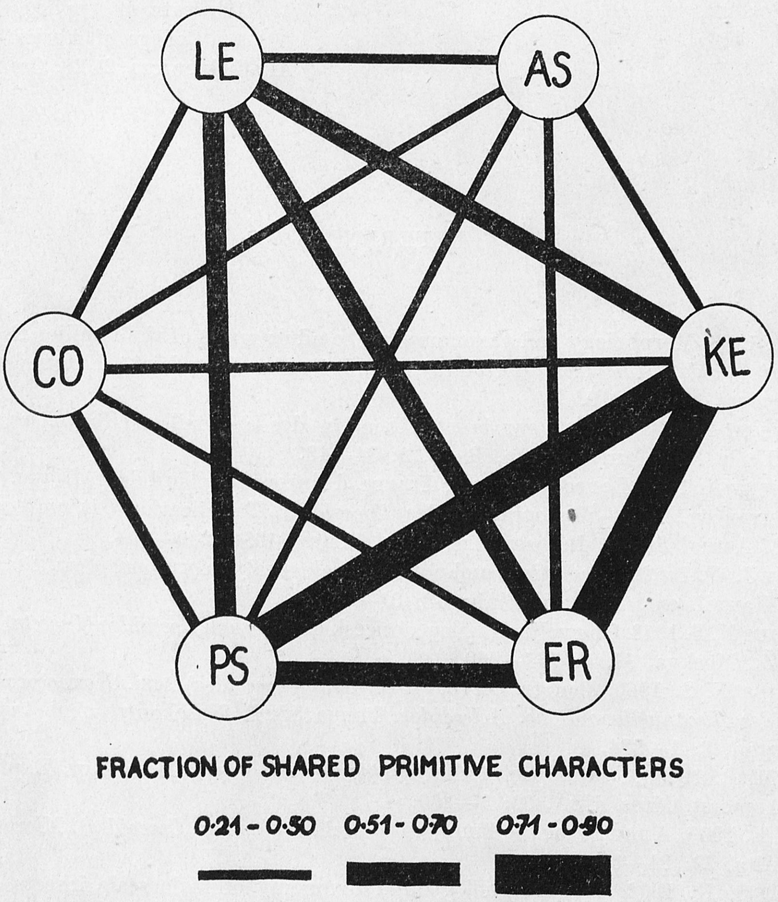


Fig. 4. The nature of the relationships between the families of the lecanoid *Coccoidea*. The width of the lines connecting the families resemble the fractions of the shared primitive characters, (see p. 10). AS — *Asterolecaniidae*, CO — *Coccidae*, ER — *Eriococcidae*, KE — *Kermesidae* LE — *Lecaniodiaspididae*, PS — *Pseudococcidae*

resemblances to some families of the lecanoid group as independently developed convergences.

The primitive lecanoid *Coccoidea* probably developed into 3 branches:

a. one led to the contemporary *Pseudococcidae*,

b. the second to the *Eriococcidae*, from which at an early stage the *Kermesidae* were isolated,

c. the third to the *Lecaniodiaspididae*, *Coccidae*, and *Asterolecaniidae*, the last one having been separated very early, and the other two being very closely related to each other.

The above scheme coincides in the main with BORCHSENIUS' (1958) views, based essentially on the structure of the females.

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STRESZCZENIE

Niniejsza praca należy do serii publikacji, których przedmiotem jest budowa struktur kutikularnych samców czerwców oraz rozważania na temat stosunków filogenetycznych w obrębie tych owadów.

Obecne badania wykazały, że rodzaj *Kermes* Boitard należy bez wątpienia do grupy czerwców nazwanej w systemie Balachowsky'ego *Lecanoidae*, ma bowiem wyraźnie wyodrębnioną głowę, a ramiona tentorium łączą się z apofyzą czaszkową.

Potwierdziły one również poglądy tych autorów (Maskall 1883, MacGillivray 1921, Borchsenius 1960), którzy rodzaj *Kermes* wyodrębnili w osobną

rodzinę. Ma on następujące cechy nie spotykane u innych czerwców wymienionej grupy: (a) listewki przedoczne (preocular ridge) są bardzo silnie wykształcone i na stronie brzusznej połączone, tak że skleryt oczny jest całkowicie oddzielony od przedniej części głowy, kiedy równocześnie listewka środkowa (midcranial ridge) jest bardzo silnie zredukowana, (b) ostatni człon czułków jest baryłkowaty, (c) ósmy sternit odwłokowy ma kształt silnie zesklerotyzowanej płytki opatrzonej po bokach listewkami, które z tyłu łączą się stawami z kapsułką genitalną, natomiast z przodu związane są listewką poprzeczną (Fig. 1, 2).

Ponadto samce omawianego rodzaju charakteryzują się bardzo silną sklerotyzacją odwłoka, spotykaną tylko u niektórych gatunków czerwców.

Dla zbadania stosunków między *Kermesidae* i innymi rodzinami „*Lecanoidae*" porównano 46 cech u *Pseudococcidae*, *Eriococcidae*, *Coccidae*, *Lecaniodiaspididae*, i *Asterolecaniidae* (Tab. I i II, Fig. 3 i 4). W obrębie tych rodzin *Kermesidae* zajmują niejako pośrednie miejsce pomiędzy *Pseudococcidae* i *Eriococcidae* z jednej, a pozostałymi rodzinami z drugiej strony. Z pierwszą grupą łączą je raczej cechy pierwotne, z drugą natomiast cechy specjalizacyjne. Nie oznacza to jednak, że *Kermesidae* miałyby być ogniwem pośrednim w sensie filogenetycznym pomiędzy *Pseudococcidae* lub *Eriococcidae* a którąkolwiek z rodzin tej drugiej grupy. Autorzy widzą w *Kermesidae* grupę spokrewnioną z *Eriococcidae*, a liczne cechy specjalizacyjne łączące ją z *Lecaniodiaspididae* i *Coccidae* traktują jako powstałe w drodze konwergencji. Podobny pogląd wyrażony został również przez niektórych badaczy w oparciu o budowę samic (Borchsenius 1958)

РЕЗЮМЕ

Настоящая работа принадлежит к числу публикаций, в которых рассматривается строение кутикулярных структур самцев кокцид, а также филогенетические соотношения в сфере этих насекомых.

Наши исследования показали, что род *Kermes* Boitard несомненно принадлежит к группе кокцид, названной в системе Balachowsky „*Lecanoidae*" так как имеет чётко выделённую голову, а ответвления тентория соединяются с черепным апофизом.

Подтвердили они тоже взгляды тех авторов (Maskell 1883, MacGillivray 1921, Borchenius 1960), которые род *Kermes* выделили в отдельное семейство. Обладает он следующими признаками не встречаемыми у других кокцид названной группы: а) предглазные дуги (preocular ridge) очень сильны и на брюшной стороне соединены, так что склеротизированная поперечная полоса головы полностью отделена от передней части головы и в то время средняя дуга (midcranial ridge) резко редуцирована, б) последний членик усиков бочковатый, в) восьмой стернит брюшка имеет форму сильно склеротизированной пластинки, снабжённой по бокам рубчиками, которые сзади соединяются суставами с генитальной капсулой, спереди же связаны поперечным рубчиком (Рис. 1, 2).

К тому же самцы рассматриваемого рода характеризуются склеторизацией брюшка, встречаемой только у некоторых других видов кокцид.

Для исследования соотношений между *Kermesidae* и другими семействами „*Lecanoidae*" было сравнено 46 признаков у *Pseudococcidae, Eriococcidae, Coccidae Lecaniodiaspididae* и *Asterolecaniidae* (таблица I и II, Рис. 3 и 4). В пределах этих семейств *Kermesidae* занимают как будто среднее место между *Pseudococcidae* и *Eriococcidae* с одной, а остальными семействами с другой стороны. С первой группой объединяют их вернее всего первичные признаки, с второй специализированные черты. Это, однако, не обозначает, что *Kermesidae* были бы средним звеном в филогенетическом смысле между *Pseudococcidae* или *Eriococcidae* и которым-нибудь из семейств этой второй группы. Авторы видят в *Kermesidae* родственную группу с *Eriococcidae*, а многочисленные специализированные черты, объединяющие её с *Lecaniodiaspididae, Asterolecaniidae* и *Coccidae,* рассматривают как возникшие путём конвергенции. Похожее мнение было выражено тоже некоторыми исследователями на основе строения самок (BORCHSENIUS 1958).

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